On Amphilina paragonopora, sp. n., and a hitherto undescribed Phase in the Life-History of the Genus.

By

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With Plates 3–5.

Contents.

Part I.

The Structure and Bionomics of Amphilina paragonopora, sp. n.

The new species of Amphilina which forms the subject-matter of this paper constitutes the fifth [1] known to exist and the third to be described in detail. I have supplied a detailed description of the anatomy of this new species because it appears to me that the descriptions of Amphilina supplied by previous authors leave much to be desired in certain respects, because the present species differs in several particulars from A. foliacea, and A. liguloidea, and because it is necessary to elucidate the exact nature and mode of function of the proboscis apparatus—the proboscis, the enormous attached proboscis muscle (or bundle of gland-ducts according to one interpretation), and the conspicuous giant cells which Salensky termed ' problematische Zellen '—an apparatus which has been much misdescribed and misunderstood. I am also able to describe an important phase in the life-history of this form, which has not been mentioned in connexion with any other species of Amphilina or, indeed, Cestodaria, so far as I am aware.

I may add that A. paragonopora is the second species of Amphilina discovered in or near India. The first (A. magna) was found by Southwell (8) in the coelom of a marine fish (Diagramma crassispinum) from the coast of Ceylon, and in general shape and structure is apparently similar to A. paragonopora, and it is to be regretted that Southwell's sole description of its genitalia is so vague. A. paragono-

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[1] The other four are A. foliacea, Rudolphi, 1819 (vide Salensky, 7; Cohn, 1; Hein, 2; Pintner, 6; Wagener, 9) and A. neritina, Salensky, 1874 (7), from Europe; A. liguloidea, Diesing, 1850 (vide Monticelli, 5; Janicki, 3), from Brazil, and A. magna, Southwell, 1915 (8), from Ceylon. The anatomy of A. neritina (assuming it to be a distinct species) is apparently very similar on the whole to that of A. foliacea, only differing in small details, and Southwell has only roughly indicated the general disposition of the genitalia in A. magna.

pora, as will be stated, is found in a fresh-water fish in the Ganges and Jumna.

(a) Habitat and External Characters.

Amphilina paragonopora is parasitic in the body-cavities of the two closely related species of Siluroid, Macrones aor and M. seenghala[1]—the common ' Tingra '—found in the Ganges and the Jumna at Allahabad and elsewhere in the United Provinces and in the Panjab, and supplied to the bazaars as food for the lower caste natives. In size the parasite varies greatly according to its stage of growth and the degree of contraction of the body musculature. The largest specimens (two) I have found measured when living (and uncontracted) 280 mm. in length (when preserved the specimens contracted to 170 mm.) and 5 mm. in maximum breadth ; on the other hand, the smallest specimens only measured 10 mm. or 11 mm. in length and 1 mm. in breadth. Specimens measuring 60–70 mm. in length are fairly common ; occasionally specimens are found which are slightly broader in proportion to their length than the above measurements indicate. The parasites are thus distinctly ribbon- or strap-shaped (Pl. 3, fig. 1), the thickness being one-fifth to one-tenth of the breadth. There is no scolex, but the ' anterior '[2] end tapers slightly, is either rounded or pointed (according to the state of contraction), and carries a short muscular globular or ovoid evaginable organ (Pl. 3, fig. 1, k)—the ' proboscis '— which is not a sucker (acetabulum) and is never used for

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[1] The chief distinction between Macrones aor and M. seenghala is that in the latter the maxillary barbels are much shorter than in the former. These fishes are said to grow to a length of six feet, but my largest specimens did not exceed three feet and the majority were between one foot and two feet in length. I may add that the food of these fishes consisted of insects (chiefly Orthoptera) and small fishes, and an examination of the tissues of this food fauna may reveal later the intermediate host or hosts of Amphilina paragonopora.

[2] I apply the term ' anterior ' to the mobile end of the body possessing the proboscis in a descriptive and not in a comparative morphological sense.

attachment. The ' posterior ' extremity of the body is similar in form to the anterior, save that at the extreme end a well-marked bay or semicircular inlet is situated, in the centre of which is a contractile papilla which bears the three separate openings of the ductus ejaculatorius, terminal excretory duct, and vagina (Pl. 3, figs. 1 *l*, 11, 12). In colour the parasites vary from a creamy-white to orange-yellow (the usual colour being a distinct yellow), and are almost always identical in tint with the masses of fat attached to the mesentery of the fish they infest.

The above statements concerning the dimensions and shape of the parasites are based on the appearance of the parasites when the body-cavity of the fish is first opened. So long as the parasites are not disturbed they exhibit no active movements, save perhaps a to-and-fro motion of the protruded ' proboscis ' which is only visible under the microscope (Pl. 4, fig. 15), but if a parasite be removed from the body-cavity and placed on a glass slide the body almost immediately shrinks to about one-half its former length and also becomes pinched by two, three, four, or more deep transverse constrictions [1] which usually travel down the body antero-posteriorly, new constrictions appearing anteriorly as the old disappear posteriorly (Pl. 3, fig. 1, *f*, *g*, *h*) ; the ' proboscis ' also either becomes extruded (Pl. 4, fig. 15, *a*) and active in penetration movements, or (more usually, especially when the animal is placed in water) becomes tightly retracted and immobile (Pl. 4, fig. 15, *b*).

Amphilina paragonopora is, as I have already stated, usually found in the body-cavity of the fish. I have most frequently found it on the mesentery, or on the peritoneum, or on the surface of the liver. On some occasions I have found specimens lying underneath the peritoneum, and once a specimen, 40 mm. in length, was discovered lying immediately dorsal to the gas bladder, in the dense connective

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[1] Hein has described similar contractions as occurring in A. foliacea, but states that they are feeble (the worm is very broad) and move postero-anteriorly, i. e. in the reverse direction to that described in the text (!).

tissue attaching the bladder to the dorsal muscles and vertebral column. Another Amphilina, 200 mm. long, was found to have bored through the wall of the gas bladder into its cavity, half the worm being in the cavity and half still outside, and another large Amphilina was found to be buried in the muscles of the body-wall anteriorly. A. paragonopora is also occasionally to be found on the external surface of the fish, and my attention was first drawn to the parasite by discovering part (56 mm. long, and a portion anterior to this, including the proboscis, of unknown length, had become detached) of a large specimen emerging from a perforation at the base of the left pectoral fin and lying on the outside of the skin (Pl. 3, fig. 3). On cutting open the perforation I found that a further portion of the worm (34 mm. long) lay in a cavity in the muscles of the body-wall, and that the remainder of the worm (the hind portion, 40 mm. long) lay inside the body-cavity. This Amphilina, therefore, had evidently bored its way through the body-wall in the neighbourhood of the base of the left pectoral fin (where the body-wall is very thin), and, had it not been caught in the act, would doubtless have altogether escaped from the fish. The uterus of this Amphilina (130 mm. in length plus an unknown length of anterior portion detached) was full of nearly or fully mature larvae (Pl. 4, fig. 35). In another fish also I found a small worm (only 11 mm. long) lying on (not attached to) the surface of the external skin just behind the anus. I cannot say whether or not this worm had escaped from the body-cavity of this fish, but it is possible (although the worm was of course immature sexually) since in this fish a large perforation (some 3 mm. in diameter) was found at the base of the right pectoral fin, leading into a large inflamed cavity in the body-wall and thence into the body cavity. Out of fifty-one [1] Macrones aor and M. seenghala, most but not all of which I specially examined for perforations under the pectoral fins, seven were seen to possess these perforations (situated either under the left

[1] In all I examined during this inquiry about one hundred specimens of Macrones sp., in twenty-two of which I found active Amphilina.

or the right pectoral fin, or, as on one occasion, under both).
From sixteen only of these fifty-one fishes did I obtain active
A. paragonopora.

I may also mention that no relationship exists between the
size of the fish and the degree of infestation by or size of the
active parasite, since some of my largest Amphilina have been
obtained from very small fish : thus e.g. in one Macrones
a o r 450 mm. long I found in the body-cavity my two largest
specimens of Amphilina (each 280 mm. long), also one about
40 mm. long, two 20 mm. long, one 15 mm. long, and two
10 mm. long, and in a Macrones seenghala only just
over 220 mm. long I obtained three Amphilina (70 mm.,
64 mm., and 59 mm. long), while in many other fishes, over
900 mm. in length, I obtained only one or two Amphilina
measuring not more than 20–30 mm.

In addition to what I have called the active parasite, there
also exist in a still larger percentage of the fishes masses of
tissue of various sizes and usually of irregular form which
closely resemble the parasite in colour and to some extent
consistency (Pl. 3, fig. 2). These masses, which range from
minute spheres and ovoids (Pl. 3, fig. 2, a) up to large shapeless,
often very thick, bodies (Pl. 3, fig. 2, $c–n$), are usually attached
to the mesentery, but are also to be found free in the body-
cavity, and, although of the same colour, yet can easily be
distinguished from masses of fat by their more solid texture.
Though evidently consisting of the same kind of tissue as the
parasites, yet they can usually be easily distinguished from
these, not only on account of their lack of definite form, but
by the fact that they cannot be flattened out between glass
slides. In some cases the connexion between these masses
and the parasites is betrayed by parts of these masses assuming
the characters of parts of the body of the active Amphilina
paragonopora (usually the anterior or posterior end—
Pl. 3, fig. 2, m, n), and in other cases these masses are almost
exactly similar in form to the parasite (Pl. 3, fig. 2, g, h, j, k)
and can only be distinguished by their total immobility (lack
of contractions) when removed from the fish and the fact,

already mentioned, that they cannot be flattened out between glass slides. We must, therefore, assume provisionally that these masses represent as a rule bodies which would, in the ordinary course of events, become transformed into active Amphilina paragonopora. They undoubtedly represent a phase in the life-history of Amphilina paragonopora, and they will be described and discussed in detail in Part II.

(b) The Reproductive System.

The general plan of construction of the reproductive system of Amphilina paragonopora (Pl. 3, fig. 8) is similar to those of A. foliacea (vide Pl. 3, fig. 9, adapted from the figures by Salensky and Hein) and A. liguloidea (as described and figured by Janicki), but, as we shall see later, there are a few noteworthy differences. Previous to describing the genitalia of A. paragonopora in detail, it is necessary to decide as to which surface of the animal is to be labelled ' dorsal ', since previous authors have been by no means unanimous concerning even this essential preliminary : thus e.g. while Salensky and Wagener consider that the side of the body on which the uterus arises from the ovary is the left, Monticelli assumes that it is the right (the view taken by the present writer), while other authors apparently avoid the subject. In typical mesozoan Cestoda it is the rule that the surface of the body to which the ovary is the more adjacent is to be regarded as the ' ventral ' surface ; and that the ootype is situated on the ' ventral ' side of the ovary. In Trematodes also, it is a rule that the vitelline ducts enter the ovary on its ' ventral ' aspect, whatever may be their subsequent course. If we apply these rules to Amphilina paragonopora, then Pl. 3, figs. 8, 10, 11, and 12 represent the organs as seen from the dorsal [1] aspect, as proved by the study of serial transverse sections. It will be observed from these figures that when viewed from the dorsal aspect, (a) the uterus arises from the right side of the ovary, runs forward nearly to the

[1] Wagener's ventral aspect.

anterior end of the body and returns on itself forming a loop,
then crosses posteriorly to the left side of the ovary, and again
returning on itself (making a short posterior loop to the left
of the ovary) runs forward and opens on the left [1] side of the
proboscis at the anterior extremity, and (b) the sperm ducts
lie dorsal to the uterus where they cross. These two features
are apparently common to all three species of Amphilina, and
we may therefore assume for all three species that when the
animal is so placed that the proboscis is directed away from
the observer and the uterus arises from the right side of the
ovary, we are then viewing the animal from the d o r s a l
aspect.

I will first briefly describe the genitalia of A . p a r a g o n o -
p o r a .   Pl. 3, fig. 8 shows the general disposition of the
genitalia, and the three diagrammatic sections the relative
positions (dorsal and ventral) of the various organs relative
to each other. Pl. 3, fig. 10 shows the arrangement of the
various ducts in the neighbourhood of the ovary. The oviduct
(OVD) arises from the ovary towards the right posterior corner
and, as shown, soon opens into a small spherical chamber, the
fertilization chamber (FC), into which also opens the slight
terminal dilatation of the vagina, the receptaculum seminis
(RS).   The fertilized eggs then escape from the fertilization
chamber by an opening situated close to that of the oviduct,
which leads into what may be called the zygote or fertilization
duct (ZD).   The zygote duct shortly receives the common
vitelline duct (VD) and then dilates slightly to form the recepta-
culum vitelli (RV), after which its walls become thickened and
glandular to form the shell gland (SHGL), and this portion of the

[1] Wagener figures the opening in A . f o l i a c e a as lying on the same
side of the proboscis as the first limb of the uterus, but if this was the
case his specimen must have been abnormal, since Salensky, Cohn, and
Hein all figure it on the opposite side in this species, and the opening
lies on what I designate the left side in A . l i g u l o i d e a , A . m a g n a ,
and A . p a r a g o n o p o r a .   It is a pity that Braun (Bronn's ' Thier-
reich ', Bd. iv, Abt. 1 b, 1894–1900, p. 1155) and Benham (Platyhelmia
in Lankester's ' Treatise on Zoology ', part iv, 1901, p. 100) should have
popularized Wagener's figure of A . f o l i a c e a .

duct is known as the ootype (OTP). The uterus (U) is continuous
with the ootype and is a thin-walled much convoluted duct of
wide diameter (capable of great expansion when filled with
grown larvae), considerably more than three times the length
of the entire body (taking the convolutions into account)
and having the characteristic conformation shown in the
figures—a conformation which is found in all five species of
Amphilina. The ducts lying in the proximity of the ovary—
from the receptaculum seminis to the beginning of the uterus—
are embedded in a dense cushion of connective tissue (CT),
probably protective in function. The common vitelline duct
is formed by the junction of the vitelline ducts (VD) of the
two sides of the body and all run dorsal to the ovary and
the uterus. The vitellaria (VIT) extend, as shown, in a row
along each edge of the body for nearly its entire length (Pl. 3,
figs. 8, 14).

The uterus does not contain eggs until the worm is at least
30–35 mm. in length, and then unsegmented eggs are only
present at the very commencement of the uterus, the rest of
the uterus being quite empty (observed in three specimens).
In a worm about 41 mm. long about a quarter of the first
(proximal) limb of the uterus is filled with embryos in the
blastomere stage of development—groups of four, eight, and
twelve blastomeres having been observed. In a worm circa
75 mm. long, the uterus is full of eggs in various stages of
development, but mature larvae are not present. In the worm
which I described as in the act of escaping from the fish through
the body-wall and which was more than 130 mm. in total length,
mature larvae in large numbers were found in the terminal
(third) limb of the uterus, the other two limbs containing larvae
in earlier stages of development. I may mention that I have
observed the larvae escaping from the uterus to the exterior
in an Amphilina not more than 100 mm. in length.

The testes (TES), as shown in Pl. 3, figs. 8 and 13, consist,
on each side of the body, of a row of sacs (Pl. 3, fig. 13) opening
at frequent intervals into the convoluted vas deferens (SD).
They lie just internal to the row of vitellaria, and, like these,

extend over the greater part of the body length. The two vasa deferentia unite to the left of the middle line at about the level of the hind end of the ovary, the right vas deferens crossing the ovary on its dorsal side. The common sperm duct then runs posteriorly to the left of the vagina, and just anterior to the terminal opening becomes invested by a thick coat of muscular tissue [1] (MTD) and then forms the thick-walled ductus ejaculatorius (DEJ). The arrangement of the terminal openings of the ductus ejaculatorius, vagina, and terminal excretory duct in A. paragonopora differs considerably from those of other species of Amphilina and merits careful description. Pl. 3, fig. 11 shows the general rather indeterminate appearance of these ducts as observed in flattened and therefore distorted specimens of A. paragonopora. This figure shows at least that all three ducts possess openings to the exterior which lie very close together (hence the name of the species ' paragonopora ', suggested to me by Dr. Baylis) and which are situated on the small median papilla enclosed in the bay (BAY) at the posterior extremity of the body, but to ascertain the exact inter-relationships of these ducts and apertures it is necessary to study series of horizontal and sagittal sections through this region (Pl. 3, fig. 12). Such series show (1) that the vagina opens on the dorsal side of the base of the papilla when this is extended (see Pl. 3, fig. 1, *l*) ; (2) that the opening of the ductus ejaculatorius to the exterior is terminal on the papilla (PE) ; and (3) that the opening of the terminal excretory duct (TED) is also terminal on the papilla and lies, so far as I can ascertain from sagittal sections and flattened whole-mount specimens, just to the left of the opening of the ductus. In some specimens the opening of the excretory duct appears to be confluent with that of the ductus. Thus all three openings lie very close together—so close that for a long time I thought they were all confluent. I may add that the excretory duct is situated ventrad to the ductus ejaculatorius where the former crosses the latter, and that

[1] This is commonly called a ' prostate gland ', but there is certainly no evidence of its glandular nature in my preparations.

the tip of the ductus is markedly thick and muscular, forming a penis. There is no conspicuous cirrus sac and no penial setae.

I will now briefly note some differences which exist between the genital system of A. paragonopora, as just described, and the genital systems of A. foliacea, A. liguloidea, and A. magna, as described by authors already named. All these three latter species are apparently distinguished from A. paragonopora by the fact that the vaginal aperture lies at a considerable distance apart from the penial aperture : in A. foliacea it is separated by about one-third the distance between the base of the ovary and the end of the body, and is situated on the edge of the left side (the ' right ' side of Salensky, who, according to my determination, viewed his specimens from the ventral surface) of the body ; in A. liguloidea it is separated by about three-quarters of this same distance, and, according to Janicki, is paired [1]—one opening being median and ventral and the other median and dorsal ; in A. magna Southwell figures the vaginal aperture as being separated by about one-fifth of this same distance, and lies in the middle line and it presumably opens dorsally.

In A. foliacea the posterior half of the vagina lies to the left of the ductus, but in the other three species the whole of the vagina lies to the right of the ductus. In A. foliacea the cirrus sac is not terminal but lies midway between the ovary and the opening ; in A. liguloidea the sac is figured as terminal ; in A. paragonopora there is no distinct cirrus sac. Only in A. foliacea are there penial setae in connexion with the very long penis (setae and length correlated with the lateral situation of the vagina and the distance separating the two openings ?). In A. liguloidea alone the vagina carries an anterior blind diverticulum extending anterior to the ovary—the so-called ' anterior vagina '. The testes are stated to be scattered in A. foliacea but in the other three species [2] they are linear in arrangement, lying just

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[1] Monticelli only describes a single aperture.

[2] Southwell states that the testes are ' scattered about through the

internal to the row of vitellaria on each side of the body.
In all four species the uterus opens at the extreme anterior
end on the left side at the base of the protruded proboscis
(Pl. 4, fig. 16).[1] Some small differences may exist in the
arrangement of the ducts adjacent to the ovary in the different
species, but, judging from the (in some cases rather doubtful)
figures, the general arrangement found in A. paragonopora
is found in all. I may add that the ventral position of the
vitelline ducts relative to the uterus shown in Hein's fig. 14
(correctly indicated as dorsal in his fig. 13 however), and
relative to the sperm ducts and the ovary shown in Janicki's
figs. 5 and 6, is probably an error in both cases—in both cases
the vitelline ducts should be shown as dorsal to these organs.

(c) The Proboscis: its Musculature and Connexions.

When A. paragonopora is removed from the body-
cavity of a freshly opened fish and placed on a slide in body-
cavity fluid, the extreme anterior end of the worm is sometimes
seen to be protruded into a narrow process which moves
vigorously from side to side in groping movements (Pls. 3, 4,
figs. 1, k, and 15, a). More usually, however, this protrusible
portion of the anterior end is not visible, it having been tightly
retracted inside the body-contour (Pl. 4, fig. 15, b). This pro-
trusible portion of the anterior extremity I shall term the
' proboscis ', and, as will be seen, it is essentially an introvert
in structure. In three or four of my specimens the proboscis
chanced to be preserved in a protruded condition (Pl. 4, fig. 16),
while in all the others the proboscis was retracted (Pl. 4, fig. 17).
From these figs. 16 and 17 it will be seen that the proboscis
essentially consists of a thickening of the wall at the extreme

parenchyma ' in A. magna, but his figure shows that the arrangement
of the testes is linear, as in A. liguloidea and A. paragonopora.

[1] I am unable to understand why Southwell (8, p. 327) supposes that
A. foliacea has no uterine opening ' at the base of the small anterior
end of the worm '.

anterior end of the worm to form a thick-walled invaginable conical bulb (Pls. 3, 4, figs. 1, *k*, and 16). In transverse section (Pl. 4, fig. 18) it can be seen that the cavity of the retracted bulb is star-shaped in outline, and in longitudinal sections of the protruded proboscis it is seen that the portion of thickened wall at the very extremity of the worm forms a kind of terminal cushion (Pl. 4, fig. 16, TT). The lateral walls of this bulb resemble the ordinary body-wall in general histological structure, but there are three very striking and significant differences, and had one of these been observed by previous writers, the true function of the proboscis and the huge so-called ' retractor ' muscle attached to it would have been obvious. The first difference is the total absence of circular and longitudinal muscle-layers, the second is the presence of very distinct large r a d i a l muscle-fibres (Pl. 4, fig. 16, RTM) which extend up to the base of the cuticle (Pl. 4, fig. 19), and the third the minute but well-marked serration of the cuticle (SER) which covers the greater part of the outer surface of the protruded proboscis (Pl. 4, figs. 16, 16 *a*) but not the terminal thickening (TT), which is altogether devoid of a cuticle. This serration of the proboscis cuticle has not been previously observed. With regard to the second difference mentioned, the radial fibres (RTM) which originate immediately under the serrated cuticle at first run longitudinally, i. e. parallel with the cuticle (Pl. 4, fig. 16, *a*), but soon bend nearly at right angles [1] and run direct to the surface of the big muscle (BM) shown in Pl. 4, fig. 16 as occupying the axis of the proboscis and then bend again and run parallel to the surface of the big muscle posteriorly, and at the hind end of the proboscis these muscle-fibres diverge, extend posteriorly in the general parenchyma of the central core of the body for a considerable distance, and finally apparently become continuous with the parenchyma. It is difficult to determine how far these fibres extend posteriorly because they are not easily distinguishable from the ordinary

[1] Some anteriorly attached fibres do not bend but run longitudinally in the proboscis wall, crossing the greater number of fibres in so doing. They do not form a layer of longitudinal muscles.

longitudinal musculature of the body. These muscle-fibres constitute the true retractor muscle of the proboscis (RTM), and are very similar in form and disposition to the retractor muscle-fibres of the proboscis of a simple Turbellarian, e.g. Pseudorhynchus bifidus, v. Gr. The terminal thickening (TT) of the proboscis consists mainly of short columnar cells and forms a thin cellular pad covering the anterior extremity of the huge axial muscle just referred to (Pl. 4, fig. 16, BM). It is to be remarked that this introvert proboscis does not possess extraneous radial protractor muscles attached to the body-wall.[1]

Occupying the central axis of the proboscis is the huge muscle (Pl. 4, fig. 16, BM) which is so conspicuous in Amphilina and which previous authors have either labelled ' retractor ' or, in view of its disproportionate size to the minute proboscis which it was supposed to retract, have regarded as a bundle of gland ducts ! Before discussing, however, the views of previous authors, I will describe the entire apparatus of the proboscis. The huge muscle can be seen to extend posteriorly as far back as the anterior end of the ovary (Pl. 4, fig. 20), its shiny fibres showing plainly in whole mounted specimens of the worm. Anteriorly, i. e. in the anterior fifth of the body-length, it is of considerable thickness and occupies at least the middle third of the body seen in transverse section (Pl. 3, fig. 5), but more posteriorly it becomes attenuated (Pl. 3, fig. 4) and immediately in front of the ovary only consists of a few centrally situated fibres. Each of these fibres (some nearly as long as the worm itself) can be seen, if traced through serial sections, to run parallel with the central longitudinal axis of the body for the greater part of its length, but just before its termination it always bends at right angles (i. e. becomes more or less radially disposed in a transverse section) and becomes connected with one of the remark-

[1] Cohn figured extraneous radiating protractor muscles in his drawing of the proboscis of A. foliacea, but they certainly do not exist in A. paragonopora. Salensky provides what is probably a much more accurate figure and shows no extraneous muscles.

able giant cells which Salensky labelled 'pro-
blematic'. The 'problematic cells' of Salensky are then
simply the attachment or 'anchor'-cells of the large axial
muscle. The mere distribution (as seen under a low-power
objective) of these anchor-cells, as I shall call them, is evidence
that they have something to do with the fibres of the muscle,
since in the anterior fifth of the body in which the muscle-fibres
are most numerous, the anchor-cells are most plentiful and
extend laterally to the region of the testes (Pl. 4, fig. 21);
whereas, more posteriorly, where the muscle-fibres are much
fewer in number, the number of anchor-cells is also much smaller
and is obviously roughly proportional to the number of fibres
in any given zone (Pl. 4, fig. 21). The continuity of the giant
anchor-cells (each as big as the egg-filled uterus in transverse
section) with the fibres of the muscle can be easily seen both in
longitudinal and transverse serial sections, whereas in whole
preparations it is not easy to see the connexion, and this accounts
for the erroneous supposition of Salensky that the processes
from these 'problematic' cells become sooner or later attenuated
and indistinguishable from the ordinary parenchyma with
which they are connected, since he doubtless did not trace
these processes through serial sections. All these anchor-cells
are elongated and their long axes in all cases lie in a plane at
right angles to the long axis of the body (Pl. 3, figs. 4, 5)—
a significant fact. These long axes are, in the case of cells
occupying the axial region of the body, disposed vertically
(the muscle processes arising from either their dorsal or ventral
ends—Pl. 3, fig. 4), but anteriorly, in those cells which are
situated nearer the sides of the body, the long axes are often
obliquely inclined towards the median axis (Pl. 3, fig. 5).
Cytologically the anchor-cells are, as Salensky remarked, not
unlike nerve-cells, and, indeed, they may be neuro-muscular
in function, though they apparently have no connexion what-
ever with the main nervous system of the worm. Each cell
(Pl. 4, figs. 22, 23) contains a nucleus (with a conspicuous
nucleolus) which lies in a small island of chromatophil cyto-
plasm (very evident in indigo-picro-carmine preparations, in

which the island is stained red and the rest of the cell-plasm
green), and the remainder of the cell is packed with con-
spicuous granules. The cell process grows out from one pole
of the cell and at first is packed with granules identical with
those in the cell, but at some distance from the cell the substance
of the fibres becomes longitudinally striated (the striations being
sinuous when the muscle is not fully extended) and much less
granular ; in other words, comes to resemble muscle-substance
(Pl. 4, fig. 24). Another and very significant fact to be men-
tioned concerning the fibres of the big muscle is that, in the
proboscis and for some distance below it, these fibres, at least
in many cases, run obliquely, as is proved by the fact that the
fibres are seen to be cut transversely or obliquely in longitu-
dinal sections cut parallel with the long axis. Pl. 4, fig. 25
gives some indication in very diagrammatic form of the
general arrangement of the muscle-fibres and their connexion
with the anchor-cells—an arrangement also found in A.
foliacea and A. liguloidea and probably in A. magna.

What can be the function of this huge axial proboscis muscle ?
Its extraordinary size enables us at once to dismiss the idea
that it is simply the retractor muscle of the minute proboscis,
as supposed by Salensky [1] and other authors, especially in
view of the fact that a well-defined retractor muscle (indicated
in A. liguloidea by Janicki in his Text-fig. 9) already
exists. In no other worm do we find a proboscis, of the size
found in Amphilina, associated with a muscle (known to be
a retractor) of the dimensions just described. In Turbellaria
the small proboscis is always retracted by a small retractor
muscle consisting of short diverging fibres ; on the other hand,
when, as in the Nemertines, the retractor muscles are long,

[1] Salensky described the fibres of the proboscis muscle as originating
posteriorly in two halves from the lateral subcutaneous muscle-layer,
and naturally could offer no explanation of the presence of his ' problematic
cells '. Hein and Cohn both failed even to find the anchor-cells (the former
confusing them with the myoblasts and the latter assuming that they were
in part identical with his flame-cells and in part ' Kunstprodukte ' !)
though these cells can be easily seen under a magnification of 30 diameters
and less.

the proboscis is also long, and even in the T e t r a r h y n c h u s
s c o l e x in which the four retractor muscles of the four pro-
boscides reach, as in Amphilina, to the hind end of the
' segment ', each proboscis is at least one-fifth the length of
its retractor muscle.

Wagener (1858) and Lang (1881), on the other hand (neither
of whom can be supposed to have recognized the fact that the
fibres of the large proboscis ' muscle ' are individually con-
nected with the giant cells which Salensky called ' problematic '),
adopted the view that the whole of the proboscis ' muscle '
is a bundle of elongated ducts connected with ' Speichel-
drüsen ' (!) lying in the parenchyma, the ducts being supposed
to open on the surface of the proboscis. Needless to say,
apart from the superficial resemblance of the anchor-cells to
gland-cells (and ganglion-cells !), and the necessity of adopting
an alternative to the ' retractor ' theory, there is no justifica-
tion whatever for this view, though it has been adopted both
by Pintner and Janicki and referred to in such well-known
general works as Bronn's ' Thierreich ' and Lankester's
' Treatise on Zoology '. The three obvious facts (evident in
any series of well-stained longitudinal sections through the
proboscis), viz. (1) that there is no trace of a lumen in the
individual fibres, (2) that the fibres are distinctly composed of
muscle substance, and (3) that the supposed ducts do not reach
the surface of the proboscis,[1] are sufficient by themselves to
dismiss this gland-complex theory, quite apart from the further
facts, already described, of the greater part of the proboscis
being covered with serrated cuticle (the terminal cushion
provides far too small an area for the openings of such a large
number of supposed ducts) and the suggestive twisting of the
muscle-fibres anteriorly, and the consideration that it is
difficult to conceive the necessity for the existence of such an
enormous gland—a gland which, with its ducts, extends
throughout nearly three-quarters of the substance of the body.

The proboscis muscle then, being neither a retractor nor

[1] Janicki, in his fig. 9 of the ' vordere Körperspitze ', expressly refrains
from figuring the supposed ducts of his ' Frontaldrüsenzelle ' !

a bundle of gland ducts, can only be associated with some special function of the proboscis. The proboscis, as we have seen, is not an organ of attachment—a sucker—but it is, on the other hand, a very efficient organ of penetration. Amphilina, as already related, normally bores its way through the tough body-wall of the fish in order to liberate its larvae to the outside world, and we know that it also occasionally bores through muscles, the wall of the gas bladder, the kidney, and other organs and tissues. But in order to overcome resistance a penetrating organ must possess (1) some degree of rigidity, (2) some instrument with which to tear tissue, and (3) a powerful muscle to work the apparatus. The large proboscis muscle—which I shall in future term the b o r i n g m u s c l e (BM)—fulfils requirements (1) and (3), and the serrated cuticle covering the outside of the protruded proboscis fulfils requirement (2). The anterior thickness of the boring muscle not only supplies the proboscis with a dense more or less rigid core with which the animal can push its way into resistant tissue, but the posterior extension and firm attachment of the muscle to the large anchor-cells firmly embedded in the axial parenchyma (and placed at right angles to the length of the fibres) enables the worm to ' put its whole weight ' into the boring process and to draw the hind portion of the body through the perforation or path made by the proboscis. The slight twisting of the fibres of the boring muscle in and below the proboscis also doubtless serves for a semi-rotary movement of the proboscis, enabling the serrated cuticle to saw its way through the tissue. The proboscis muscle thus serves as a boring muscle, as a notochord for the anterior end of the body and as a means of dragging the hind half of the body along the path excavated by the proboscis, and these important functions amply account for its huge size. Retraction of the proboscis is effected by the retractor muscle, and protrusion of the proboscis probably results merely from the slackening of the retractor (the stiff boring muscle naturally projecting forwards in a position of rest) but possibly also from the contraction of the longitudinal muscles attached to

the body-wall at the base of the proboscis—the proboscis
being exposed by this means.

(d) The Excretory System.

Salensky has described the presence in Amphilina
foliacea of two lateral excretory channels (lying one on
each side of the body internal to the nerves) which receive
branches from the parenchyma. This description agrees
essentially with the plan of excretory system which I have
found in A. paragonopora, and I therefore venture to
doubt the accuracy of Hein's account (with figures) of an
irregular close network of excretory channels occurring in
A. foliacea.[1] In A. paragonopora, as in A. foliacea,
a large excretory channel extends along the whole length of each
side of the body, lying immediately internal to the testes (Pl. 3,
fig. 6). Anteriorly (Pl. 4, fig. 17) each channel apparently
originates as a narrow channel or loop (equal in calibre to one
of the branches or loops given off more posteriorly) in the
parenchyma situated at the sides of the base of the proboscis ;
posteriorly the two lateral channels converge and meet in the
middle line in a slight dilatation (situated at about a third
of a millimetre from the terminal aperture—Pl. 3, fig. 12, EXB)
to form the terminal single excretory duct (TED), which in its
turn runs directly to open externally on the papilla (PAP)
at the extreme posterior end of the body, the opening lying
adjacent to and to the left of that of the penis. In addition
to these two lateral main excretory channels there are four
series of subsidiary (as regards size) excretory channels, which
arise from the two lateral main channels along their entire
length. The first that may be mentioned comprises the
dorsal transverse channels (Pl. 3, figs. 4, 6, DTC),
which put the two lateral main channels into direct communica-
tion across the dorsal side of the body, lying between the

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[1] I am aware that Cohn speaks of definite lateral channels and a net-
work in A. foliacea, and that Janicki figures a fine network in
A. liguloidea.

internal longitudinal muscle-layer and the dorsal anchor-cells and fibres of the boring muscle ; the second series comprises the similar transverse channels situated on the ventral side of the body—the v e n t r a l   t r a n s v e r s e   c h a n n e l s (Pl. 3, figs. 4, 6, vtc) ; the third comprises those channels which arise from each lateral main channel on its dorsal side and turn outwards towards the outer edge of the body—the d o r s a l e x t e r n a l   c h a n n e l s (Pl. 3, fig. 4, dec) ; and the fourth comprises the similar outwardly directed channels which arise from the ventral side of the lateral main channel—the v e n t r a l   e x t e r n a l   c h a n n e l s (Pl. 3, fig. 4, vec). In many and perhaps in most cases, the dorsal external channels and the ventral external channels join together to form a l a t e r a l e x c r e t o r y   l o o p (Pl. 3, fig. 6, lel), but in other cases the two channels do not appear to communicate. Thus, in its main plan, the excretory system consists (1) of two lateral main channels which unite posteriorly to form a single exit channel which opens to the exterior at the posterior extremity, and (2) of subsidiary smaller channels which take the form, roughly speaking, of three series of ' rings '—the axially situated series of flattened ' rings ' formed by the dorsal and ventral transverse channels, and the two lateral series of ' rings ' arising from and lying external to the lateral main channels. It must be mentioned, however, that the upper and lower halves of these ' rings ' very rarely lie in the same transverse plane—they only form a ' ring ' when a considerable thickness of the body is viewed end-on. In one worm measuring about 40 mm. in length I observed that in 5 mm. of this length approximately 21 external channels were given off from one of the lateral main channels—about 150 in the entire length of the worm.

Apart from this system of channels I have been unable to discover any other portion of the excretory system, though I have searched most carefully, in both transverse and longitudinal series of well-fixed sections, for flame-cells. According to Hein and Cohn flame-cells exist in A .   f o l i a c e a in large numbers, and the former author figures them ; but these statements need confirmation, since Hein is possibly mistaken

in his description of the general plan of the excretory system and admits that his preparations were ill adapted to show even the central nervous system ; and Cohn, as we have seen, suggested that Salensky's ' problematic ' cells were themselves the flame-cells ! I may add, finally, that I was also unable to detect cilia in any of the excretory canals.

(e) The Central Nervous System.

In 1874 Salensky remarked upon the presence in A m p h i - l i n a f o l i a c e a of two longitudinal nerve-trunks, and Lang (4) in 1881 confirmed this, and also described a ' brain com- missure ' (a band of fibres piercing the boring muscle) and branches given off from the two lateral longitudinal trunks. Cohn in 1904 added the information that the branches given off dorsally and ventrally from each of the two lateral longitu- dinal trunks meet dorsally and ventrally across the body so as to form a series of nerve-rings throughout the length of the body, but since these rings were not observed by Lang, and are certainly not present in the elongated and more nearly cylindrical A. p a r a g o n o p o r a, I doubt their existence. Pl. 4, fig. 29 illustrates the anterior end of the central nervous system in A. p a r a g o n o p o r a, and it will be seen that it confirms Lang's description in all respects. Anterior to the ' brain commissure ' the two lateral longitudinal trunks extend forwards and end in the margin of the anterior end of the body. Posteriorly, in A. p a r a g o n o p o r a, the two lateral longitudinal trunks converge slightly (in accordance with the narrowing of the body) but do not appear to join : they terminate separately at the sides of the posterior inlet or semicircular bay at the posterior end, in much the same way as the trunks terminate anteriorly. In transverse and longitu- dinal sections each of the lateral longitudinal trunks is seen to give off dorsal, ventral, and internal branches (Pls. 3, 4, figs. 4, 5, 29), and these are distributed to the body-wall muscles and other organs. I have not ascertained the exact numbers of these branches. The trunks are uniform in diameter and there are no special aggregations of ganglion cells.

(f) The Histology of the Body-wall and the Body Musculature.

Pl. 4, fig. 26 shows the appearance of the body-wall in transverse section. The cuticle (cut) is not very thick, and immediately underlying it is the thick 'subcuticula' (subc). The outer zone of the subcuticula apparently consists solely of numerous radially disposed thin fibres similar in nature to those which compose the general parenchyma. Three muscle-layers lie in the outer zone of the subcuticula—the thin outer circular muscle layer (ocm), a thin layer of longitudinal muscle-fibres (olm), and a second thin layer of circular fibres (icm). Internal to these three muscle-layers lies the inner zone of the subcuticula ('epidermal' layer), consisting of spindle-shaped cells, in between which lie radially-disposed fibres and numerous calcareous bodies (calc). Underlying the subcuticula is the parenchyma (par), in the outer zone of which lies a powerful longitudinal muscle-layer (ilm), and internally to which there is to be seen an attenuated scattered layer of oblique longitudinal muscle-fibres (oblm). Gland-cells (gc), excretory canals, and nerve-fibres (nfi) are also of course contained in the parenchyma. Included in this Pl. 4, fig. 26 is a drawing of a giant anchor-cell (ancc) drawn to the same scale, which will give some idea as to the enormous size of this class of cell. Pl. 4, fig. 27 illustrates a longitudinal section through the body-wall, and this shows the indentations of the cuticle and subcuticula due to the outer substance of the body-wall being ridged transversely when contracted longitudinally.

(g) Some Stages in the Development of the Larva.

The mature eggs in the ovary which are about to enter the oviduct in an Amphilina paragonopora about 30 mm. long are of the ordinary alecithal type. After having been fertilized and passed through the ootype, the eggs normally become encased, with a quantity of yolk material, in a relatively thin irregularly oval shell, to one end of which is attached

a short filament or ' tag ' (Pl. 4, fig. 30, *f*). Occasionally eggs
are shed into the uterus without a shell. Only unsegmented
eggs are to be found in a worm about 30 mm. long, and they are
situated in the portion of the uterus immediately adjacent to
the ovary, the rest of the uterus being empty. In an older
A. paragonopora (a little over 40 mm. in length and cut
into serial horizontal sections) I have observed early segmenta-
tion stages—groups of four, eight, twelve and more blastomeres
—and in some of the early morulae it is possible to detect one
or two blastomeres which differ from the rest and which are
doubtless destined to form the investing membrane of the
embryo. In a worm a little over 70 mm. in length the uterus
is full of embryos, the oldest stage being a solid morula which
fills the shell, the morula being surrounded by an investing
membrane (Pl. 4, fig. 31 depicts a very young morula). In
another worm (87 mm. long when uncontracted, though it
shrank to 32 mm. when placed on a slide) which I cut into
serial transverse sections, the third limb of the uterus was full
of embryos of the stage represented by Pl. 4, fig. 34, while
earlier stages (e. g. that represented by Pl. 4, fig. 32, which I
drew on account of the single large internally situated blasto-
mere shown—GBL) were present in the other two limbs. The
embryos in limbs 2 and 3 of the uterus all possess a definite
ectoderm, while in limb 3 the embryos are further distinguished
(1) by the possession of a small group of large glandiform cells
(GC) which are drawn out towards one end of the embryo
and may be unicellular glands similar to those found in many
cerariae, and (2) by the elongation of the terminal cells at the
other end of the embryo (Pl. 4, fig. 33) and the secretion by
these cells of the ten (I think) calcareous hooklets so charac-
teristic of the Amphilina larva (Pl. 4, fig. 34). Pl. 4, figs. 33
and 34 are drawn from sections. In three worms each about
100 mm. long when uncontracted, the third limb of the uterus
was full of larvae still contained in their shells, which they
filled and were somewhat longer than the stage represented
by Pl. 4, fig. 34. At this stage the larvae are often liberated
and are about 100 microns in length. Pl. 4, fig. 35 represents

in optical section the type of larva found in large numbers in the third limb of the uterus in a worm more than 130 mm. long (the worm which was in course of boring its way through the fish body : vide Pl. 3, fig. 3). In these larvae (which were about 200 microns in length—twice the length of other mature larvae observed by me), whether mounted whole or in section, I found it difficult to detect for certain the central group of gland-cells which is so distinctly figured by Salensky (vide his fig. 34) and Janicki (vide his fig. 16) and which I have seen clearly in sections of younger larvae, the probable reason being that the gland-cells are much distended and full of unstained secretion : it is difficult to suppose that the gland-cells have disappeared at this stage. The anterior end of the larva (the end opposite the hooklets) is usually drawn out somewhat and probably carries the fine ducts of the gland-cells. The larva at this stage has usually escaped from its shell and has secreted a thin but definite cuticle, outside which lies the remains of the investing membrane. I could detect no trace of ciliation on any part of the surface.

The foregoing facts were, as I have stated, observed by me in specimens of A. paragonopora ranging from 30 mm. to 130 + ? mm. in length and require no particular comment. In one of my two largest specimens of this worm (both 280 mm. long when living and uncontracted), however, I found, both in horizontal and vertical longitudinal sections, in portions of the body mounted whole and in macerated preparations of the body, two types of products in the uterus (all three limbs of which apparently contained the same or similar products) : (1) oval flattened larvae (Pl. 4, figs. 38, 39) with typical hooklets and possibly with gland-cells (though I could not observe them even in sections ; however, large spheres, not shown in Pl. 4, figs. 3, 8, could occasionally be distinguished deep in the substance) and only as long as the larvae liberated from worms 100 mm. long, i. e. half the length of the larvae represented by Pl. 4, fig. 35 [1] (though the hooklets were the same size in both)

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[1] I am unable to say whether the larvae of Pl. 4, fig. 35 are abnormally large (since they were only found in a single worm) or whether the flat

and of much denser consistency, and (2) oval egg-shells but little inferior in size to the larvae and containing only a few large dissociated blastomeres of different sizes (Pl. 4, figs. 37, 39). These practically empty egg-shells were extremely numerous—from five to ten times more numerous than the oval larvae. They are best displayed by macerating portions of the Amphilina, either fresh or preserved, in Marcacci's fluid (equal parts of nitric acid, glycerine, and water) over-night, followed by teasing or, better still, by grinding up on metal gauze suspended in water with a piece of flat wood—the products of the grinding sink through the gauze and can be collected by centrifuging. Lest it be thought that the half-empty condition of the egg-shells was due to the Marcacci's fluid, I may mention that I obtained the same result with simple maceration in water (Pl. 4, fig. 39) and that Marcacci's fluid does not damage even such objects as spermatozoa ; the half-empty egg-shells can also be seen, as already mentioned, in whole-mounted specimens and in serial sections mounted in balsam. I may also mention that it was only by employing Marcacci's fluid that I first detected the filament or tag on the egg-shells, it usually being difficult to see this structure in sections and whole mounts. I suspect that similar maceration would display a tag on the egg-shells of Amphilina magna, Southwell.

The half-empty egg-shells undoubtedly represent larvae that have degenerated. It is conceivable that if for any reason a worm cannot escape from its fish host, the larvae degenerate in consequence of not being liberated into water. Facts cited in Part II afford additional evidence in favour of this view.

(h) Re-definition of the Genus Amphilina, and the chief Distinctions between the five Species.

Wagener's definition of the genus Amphilina (9) must be amended in order to comprise the facts that in A. para-gonopora the body is ribbon-shaped, the posterior end is

larvae (which are the same length as the largest larvae I have seen in utero) are abnormally small.

not pointed, the two surfaces are alike in curvature, and that the proboscis does not bear the openings of a gland complex, the latter being a large boring muscle, the fibres of which extend a considerable distance posteriorly (probably about eight-ninths of the length of the body in the three best-known species) and become connected individually with giant 'anchor'-cells. Thus amended the definition of the genus reads as follows : Body flat and varying in outline from an oval to a narrow ribbon. Anterior end pointed or slightly truncated according to the state of contraction ; posterior end pointed, rounded, or emarginate. A small evaginable proboscis is present at the anterior end, and connected with this is a large boring muscle, the fibres of which end posteriorly in giant 'anchor'-cells situated in the parenchyma. The excretory system consists usually of two main lateral channels connected with a system of smaller channels and opening posteriorly by an approximately median single pore. Testes numerous. Ovary and openings of vas deferens and vagina posterior. Uterus a long convoluted duct consisting of three limbs (N-shaped when viewed from the ventral surface), each extending nearly the entire length of the body, and opening anteriorly at the base of the proboscis and on the left side (i.e. on the side of the body opposite to that on which the uterus arises from the ovary).

I may add that in no species is there an 'acetabulate sucker'.

Some of the more conspicuous distinctions between the five known species of Amphilina are stated in the Table on the next page.

The specific distinctness of A. neritina from A. foliacea needs confirmation.

Three type-specimens (including one of maximum size) of Amphilina paragonopora have been deposited in the British Museum (Natural History) at South Kensington, London.

	A. neritina.	A. foliacea.	A. liguloidea.	A. magna.	A. paragonopora.
Colour	Grey-green	Creamy-white	Grey-white	Milky-white	Creamy-yellow to orange.
Maximum length	18 mm.	26–60 mm.	86 mm. (preserved)	250 mm. (preserved) 381 mm. (living)	170 mm. (preserved) 280 mm. (living).
Approximate ratio of maximum breadth of body (taken as 1) to length	1/2·0	1/1·2–1·30 *	1/3·5–4·0	1/10·6–12·8	1/20·8–28·3 †
Body extremities	Both ends narrow and rounded	Both ends narrow and rounded	Both ends narrow and pointed	Both ends narrow and rounded	Anterior end pointed or rounded, posterior end emarginate.
Host	Acipenser sp. Europe.	Acipenser sp. Europe.	Arapaima gigas, Brazil	Diagramma crassispinum. coast of Ceylon	Macrones aor et seenghala, rivers of North India.
Vagina and its aperture	In both species vagina lies posteriorly to left of ductus and opens on left margin of body about 2 mm. away from the median ductus opening		Vagina to right of ductus and has dorsal and ventral openings in middle line about 3 mm. from hind extremity. Vagina has anterior diverticulum	Vagina to right of ductus and opens dorsally (?) in middle line 2 mm. from hind extremity	Vagina to right of ductus and opening at hind extremity just dorsal to ductus opening in middle line.
Penial setae	?	Penial setae Said to be scattered	No penial setae	No penial setae	No penial setae.
Testes	?		Linear arrangement	Linear arrangement	Linear arrangement

* Measurements of five drawings from Salensky, Hein, and Cohn.

† In my largest living specimens the radio was 1/56.

Part II.

On the Irregular-form Stage of Development in the Life-cycle of Amphilina paragonopora.

I have already mentioned in Part I that in addition to the active Amphilina paragonopora there are to be found attached to the mesentery and, in the case of the larger bodies, lying free in the body-cavity of Macrones aor and M. seenghala, large numbers of masses of tissue, varying greatly in size and form and, except in the case of the smaller bodies, rarely showing any approach to a definite shape (Pl. 3, fig. 2), but which, nevertheless, are similar in colour to the active worm, though they differ in consistency, it being impossible to flatten them between glass slides. They are quite distinct from the similarly coloured masses of fat, being denser in appearance and texture. These amorphous [1] masses are stages in the development of the active Amphilina, a fact which is proved by the discovery of stages transitional between the two (vide Pl. 3, fig. 2, m, n), and they represent a distinct part of the life-cycle of the species. The portion of life-cycle from the formation and escape of the larva from the fish to the first appearance of the amorphous masses in the mesentery of the fish is unknown.

The smallest amorphous masses which can be detected in the mesentery by the naked eye are spherical or ovoid in shape (Pl. 3, fig. 2, a),[2] and there exist all transitions from these small masses up to elongated masses 80 mm. or more in length (Pls. 3, 5, figs. 2 and 46). I have cut serial sections of some dozens of these masses and also through portions of infected mesentery, and by close examination of these I have

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[1] I use this term, which strictly speaking can only be applied to a gas, for want of a better. So far as I am aware there is no term in use in English to express the meaning of indefinite shape as apart from definite. Professor Platt suggested ' ataxomorphic '.

[2] It is impossible to distinguish these with the naked eye from the numerous Nematode cysts which also abound.

found what are undoubtedly the earliest stages of growth of these masses, and several other facts of interest.

The earliest certain developmental stage of the amorphous mass which I have observed was approximately spherical and measured 29 microns in diameter (Pl. 5, fig. 40, ×500). The mass simply consists of a globule of plasm with a dozen or so nuclei embedded in it, and is surrounded by a relatively thick capsule of loose concentrically arranged fibres; usually capillaries are to be seen near by. I have seen about a dozen of these early stages [1] (one measuring 40·2 microns in diameter is shown in Pl. 5, fig. 41, ×500, and another larger one in Pl. 5, fig. 42, ×500). It will be noticed that these minute masses are smaller than the larvae liberated from the uterus of the worm, and it is therefore evident that the larva must undergo some process of subdivision, probably in an intermediate host, before infection of another fish can occur. I have not been able to trace these masses back to a unicellular stage. Encapsulated masses larger than these early stages are very numerous, and of course are easily distinguishable in section from small Nematode cysts of the same size both by the absence of the worm, the nature of the contents, and by the structure of the capsule wall. As I have said before, all stages of the growth of these masses are to be found, and since it would be profitless to describe the gradual process of histogenesis which commence in masses of about the size shown in Pl. 5, fig. 45, I have only figured sections of three of the later stages, the magnifications stated giving some idea of their relative sizes. Pl. 5, fig. 43 (×112) illustrates an encapsuled mass with tissue still quite undifferentiated, and Pl. 5, fig. 44 (×112) a larger similar mass, and Pl. 5, fig. 45 (×35) shows a later stage of the worm after it has become too long for the capsule and is consequently becoming coiled. The commencing histogenesis is not indicated in the figure. In still later stages

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[1] These early stages must be distinguished from sections through nerve-fibres in the mesentery, which are very numerous and are often twisted into lumps of about the same size as the masses, and in some cases are so small as to resemble unicellular bodies.

the worm becomes much more coiled inside the capsule,[1] and
at some period escapes from the capsule. Judging from the
widely different sizes, both of masses lying free in the body-
cavity and of the active Amphilina, the differentiated masses
must escape from their capsules at very different stages of
growth. It must be understood that although I have only
figured a few of the stages of development of these masses,
yet all stages transitional between the youngest and the oldest
can be observed in sections through infected mesentery. It
is evidently unnecessary to give figures of the entire series.

Two other kinds of encapsulated masses must be described. In
two of the largest amorphous masses (Pl. 3, fig. 2, *e*, represents
one of these masses) I found enclosed in each a histologically
well-developed Amphilina of large size and considerable
length, the body being tightly coiled on account of the restricted
space. Many of the tissues of these encapsulated Amphilina
were well differentiated and especially the reproductive system,
the uterus being of large size and, to my great surprise, f u l l
of l a r g e o v a l f l a t l a r v a e w i t h t h e i r c h a r a c -
t e r i s t i c h o o k l e t s and equal in size to the similarly shaped
larvae in the uterus of the 280 mm. active Amphilina described
in Part I. The larvae, however, were very degenerate (in
most cases largely disintegrated) and were only recognizable
as larvae on account of their location, general shape, and the
characteristic hooklets. The only hypothesis which I can sug-
gest to account for these facts is that for some reason the
amorphous mass in this instance had been unable to escape
from its capsule, and being compelled to undergo its develop-
ment inside the capsule, this development was both incomplete
(e. g. the proboscis was not developed) and one-sided, the
reproductive organs developing at the expense of other organs.
The larvae being formed and unable to escape, naturally
degenerated. Certain appearances suggest to me that in
places the substance of the worm was being invaded by histo-
lytic tissue derived from the walls of the capsule.

[1] Salensky states that he once found a young A. f o l i a c e a contained
in a capsule on the peritoneum covering the liver of the Sterlet.

In one other case—an isolated instance—I found a small capsule (roughly 500 microns long and 384 microns in mean transverse diameter) also to contain a dozen or so degenerate flat larvae and some disintegrated matter, but in this case no worm was enclosed in the capsule nor could ever have been in a capsule of this small size (Pl. 5, fig. 47). The only explanation of this remarkable situation of the degenerate larvae is that the larvae had been ejected from an Amphilina into the body-cavity of the fish (and we have seen that larvae are sometimes extruded from the uterine pore long before the worm escapes from the body-cavity) and that the larvae having come into contact with the mesentery, a histolytic capsule had been formed by the mesentery tissue to isolate and destroy them (the amorphous masses are themselves surrounded by capsules formed from mesentery tissue, in much the same way that Linguatulid larvae become encapsuled). It will be noticed from Pl. 5, fig. 47 that the walls of the histolytic capsule are very different in construction from the walls of the capsules enclosing normal amorphous bodies.

It is thus of interest to note that larvae, if not liberated soon enough, can become degenerate (1) in an active Amphilina (as e. g. in the 280 mm. Amphilina described above); (2) in an Amphilina permanently imprisoned in its capsule, and (3) when liberated into but unable to escape from the body-cavity of the host (fish). The only fact which it is difficult to understand is why, in the 280 mm. Amphilina, only a small proportion of the eggs had developed as far as the full-grown larva stage, the rest becoming degenerate while still inside their shells. But perhaps this was an anomalous, as it certainly was, in my observations, an isolated, occurrence : in no other instance have I observed the uterus to contain anything but normally developing or developed larvae. I may emphasize that the flat oval type of larva seen in the 280 mm. Amphilina also occurred in the capsule-imprisoned Amphilina and in the histolytic capsule, and possibly this is the fully grown stage of the larva, the type of larva figured by Selensky, e. g., being not fully grown.

Notes on Technique.

I fixed specimens of Amphilina paragonopora either in Zenker's fluid, Mann's fluid, aceto-bichromate, or simply in 6 per cent. formalin. Some of the specimens were first flattened between glass slides, and these, when properly stained, showed the reproductive organs well. Unflattened specimens were either embedded for section-cutting (the specimens being kept straight by being placed between small squares of wire gauze while in the embedding bath) or simply preserved in formalin and glycerine. Whole specimens and sections were usually stained either with Delafield's haematoxylin (diluted with ten times its bulk of water, and immersion over-night) and in some cases followed by eosin or other plasma stain, or with borax carmine. Both stains gave good results.

In conclusion I wish to express my indebtedness to Dr. H. A. Baylis, who very kindly consulted for me, while I was in India, several original papers and checked my references to previous work, and to Dr. S. W. Kemp, who kindly sent to me some volumes from the Indian Museum library at Calcutta while I was in Allahabad. I am also indebted to Colonel G. E. F. Stammers for some assistance in checking references, and to Messrs. B. K. Das, M.Sc., and S. K. Datta, M.Sc., for the considerable assistance they have kindly given to me in obtaining large numbers of Macrones and finding Amphilina.

Summary of Principal Conclusions in Parts I and II.

1. Amphilina paragonopora is parasitic in the body-cavity of the Siluroid fishes, Macrones aor and M. seenghala, from the Ganges and Jumna, India. It is linear in shape and varies in length from about 10 mm. to 280 mm., but full-grown larvae are not formed in the worm until it is at least 100 mm. in length. The 'anterior' end of the parasite is rounded and carries a small proboscis, which is a boring organ and not a sucker. The uterus opens anteriorly to the left and at the base of the proboscis. The 'posterior' end of the body is marked by a semicircular inlet or bay, and on

a median papilla in the bay open the ductus ejaculatorius (at the extremity of the papilla in the middle line), vagina (at the base of the papilla on its dorsal side, the opening thus being practically terminal) and terminal excretory duct (immediately to the left of the opening of the ductus and sometimes confluent with it). The parasites when mature (the uterus being filled with larvae in various stages of development) apparently escape from the fish by boring through the body-wall at the base of one of the pectoral fins. In addition to the 'active' parasite, an inactive stage in its life-cycle is to be found in the form of irregularly shaped masses usually attached to the mesentery.

2. The general plan of the reproductive system is similar to that in Amphilina foliacea, but there are some note-worthy differences, already summarized at the end of Part I.

3. The small boring proboscis (covered with a serrated cuticle) is connected with and manipulated by a huge boring muscle (formerly miscalled 'retractor' by some authors, and by others interpreted as a bundle of gland ducts—the 'problematic' cells of Salensky being the glands) which is very thick anteriorly and extends posteriorly, though in an attenuated form, to the region of the ovary. The fibres of this boring muscle end in the giant cells which Salensky called 'problematic' and which I have renamed 'anchor'-cells. The function of the boring muscle is (1) to give a semi-rotary movement to the proboscis (its fibres being twisted anteriorly), (2) to act as a stout support for the anterior end of the body when engaged in boring, and (3) to drag the hinder portion of the body through the perforation made by the proboscis—and these three functions account for the enormous size of the muscle. A true and distinct retractor muscle lies externally to the boring muscle.

4. The excretory system consists of two lateral main channels which unite posteriorly and form a short straight terminal excretory duct which opens in the median line posteriorly, and a series of smaller loops and branches given off from these two lateral main channels, which appear to form, typically, three series of 'rings' when the body is viewed end-on (Pl. 3, fig. 6). Flame-cells are absent.

5. The central nervous system is, in the main, that described by Lang for Amphilina foliacea.

6. Some stages in the development of the larva are described, and the larvae, when liberated from the uterus, appear to be similar to those of Amphilina foliacea. Fully grown

larvae found in a 280 mm. specimen of A. p a r a g o n o p o r a
are oval in shape and flattened, and possibly do not possess
the large gland-cells, but these may be degenerate forms.

7. The genus Amphilina is re-defined and the more con-
spicuous specific differences between the five species of Amphi-
lina are stated.

8. A brief account of the irregular-form stage in the life-
history of A. p a r a g o n o p o r a is given, from which it
appears that the amorphous masses found on the mesentery
of the fish and which give rise to the active Amphilina, arise
from small spherical multicellular masses (about 30 microns
in diameter) enclosed in capsules formed by the mesentery
tissue. All transitions can be observed from these smallest
masses up to the stages in Pls. 3, 5, figs. 2 and 45, and thence to
the active Amphilina.

Occasionally the masses develop into sexual Amphilina inside
the capsules which enclose the masses, since Amphilina con-
taining full-grown larvae are occasionally met with inside large
capsules.

Occasionally also larvae liberated into the body-cavity
become secondarily encapsulated by the mesentery tissue and
are apparently disintegrated.

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EXPLANATION OF PLATES 3, 4, AND 5.

N.B.—The magnifications given for all figures are those at which the figures were drawn. The extent to which these magnifications have been reduced in printing can be estimated by comparison of the printed 5 cm. scale with an actual 5 cm. The majority of figures were drawn under the camera lucida.

PLATE 3.

Reference Letters in Figures 1–7.

ANCC, giant anchor-cells ; BM, boring muscle ; CALC, calcareous bodies ; DEC, dorsal external excretory channel ; DEJ, opening of ductus ejaculatorius ; DNB, dorsal nerve branch ; DTC, dorsal transverse excretory channel ; LEC, lateral main excretory channel ; LEL, lateral excretory loop ; LLT, lateral longitudinal nerve trunk ; P, perforation at base of left pectoral fin ; RTM, retractor muscle-fibres of proboscis ; TED, terminal excretory duct ; TES, testes ; U 1, U 2, U 3. first, second, and third limbs of uterus ; VEC, ventral external excretory channel ; VIT, vitellaria ; VNB, ventral nerve branch ; VOP, opening of vagina ; VTC, ventral transverse excretory channel.

Fig. 1.—*a, b, c, d, e,* outlines of young specimens of Amphilina paragonopora (drawn natural size) ; *f, g, h,* three specimens of A. paragonopora showing transverse constrictions of body when removed from the host ; *j.* an A. paragonopora which measured 280 mm. when alive and uncontracted (contracted to 170 mm. when preserved). The proboscis is evaginated ; *k,* the anterior end of the 280 mm. specimen showing the evaginated proboscis as seen under the binocular ; *l,* the posterior end of the same specimen showing the opening of the vagina (dorsal) at the base of the papilla and the opening of the ductus at the extremity.

Fig. 2 (drawn natural size) illustrates some of the immobile, mostly amorphous, masses which represent a phase in the life-history of the species ; 2, *a* represents the young spherical and ovoid masses ; in 2, *m,* one end of a large mass has assumed the form of the anterior extremity of the active worm, and in 2, *n,* the posterior extremity of the active worm is apparent.

Fig. 3 (drawn natural size).—Anterior portion of a large A. paragonopora which has escaped from the body-cavity of the fish through the perforation at the base of the left pectoral fin.

Fig. 4 (×cir. 63).—Transverse section through A. paragonopora about midway in the length of the body.

Fig. 5 (× cir. 63).—Similar transverse section at about the level of the hind end of the anterior fifth of the body.

Fig. 6 (× cir. 7).—Diagrams representing the general arrangement of the excretory channels in the anterior third of the worm and the two main channels throughout.

Fig. 7 (× cir. 950).—Portion of a very fine excretory canal.

Reference Letters in Figures 8–14.

BAY. terminal bay or inlet at hind end of body ; BM, boring muscle ; CMO. median opening of the ductus ejaculatorius ; CT, connective tissue investment of ducts ; DEJ, ductus ejaculatorius ; EXB, junction of two lateral main excretory channels ; FC, fertilization chamber ; LEC, lateral main excretory channel ; MTD, muscular tissue round ductus ; O, ovary ; OTP, ootype ; OVD, oviduct ; PAP, papilla with terminal opening of ductus ; PE. penis ; PRO, proboscis ; RS, receptaculum seminis ; RV, receptaculum vitelli ; SD, sperm duct ; SHGL, shell gland ; TED, terminal excretory duct with opening to the left of ductus ; TES, testes ; U. uterus ; U 1, U 2, U 3. first, second, and third limbs of the uterus ; UO, opening of uterus ; VAG, vagina ; VD, vitelline duct ; VIT, vitellaria ; VOP, opening of vagina ; ZD, zygote duct.

Fig. 8 (× cir. 7).—Dorsal aspect of the general reproductive apparatus of Amphilina paragonopora, with three diagrammatic transverse sections in the region of the ovary to show the relative dorsal and ventral positions of the various ducts.

Fig. 9.—Diagram of the general reproductive apparatus of Amphilina foliacea, for comparison with fig. 8.

Fig. 10 (× cir. 660).—The base of the ovary and associated ducts.

Fig. 11 (× cir. 660).—Surface view of the posterior ending of the ductus ejaculatorius. vagina. and lateral main excretory channels.

Fig. 12 (× cir. 63).—Reconstruction from serial longitudinal sections of the structures shown in fig. 11.

Fig. 13 (× cir. 330).—Testes opening into the vas deferens.

Fig. 14 (× cir. 330).—Vitellaria opening into the vitelline duct.

PLATE 4.

Reference Letters in Figures 15–25.

ANCC, giant anchor-cells ; BM, boring muscle ; CALC, calcareous bodies ; LEC. lateral main excretory channel ; O, ovary ; PRO, proboscis ; RTM, retractor muscle of proboscis ; SER, serrated cuticle of proboscis ; TES, testes ; TT, terminal thickening of proboscis ; U 1, U 2, U 3, first, second, and third limbs of uterus ; UO, opening of uterus ; VIT, vitellaria.

Fig. 15.—Sketch of proboscis everted (a) and retracted (b), drawn from the living animal.

Fig. 16 (× cir. 78).—Everted proboscis in longitudinal section.

Fig. 16. a (×1060).—Serrated cuticle covering proboscis.

Fig. 17 (× cir. 78).—Introverted proboscis in longitudinal section (drawn from a whole-mount specimen).

Fig. 18 (× cir. 150).—Retracted proboscis in transverse section.

Fig. 19 (× cir. 310).—Portion of wall of proboscis in longitudinal section.

Fig. 20 (× cir. 2).—Diagram to illustrate the longitudinal extent of the boring muscle of the proboscis.

Fig. 21 (× cir. 7).—Diagram to illustrate the distribution of the boring muscle-fibres and the giant anchor-cells (Salensky's ' problematic cells '), and the same structures shown in two transverse sections (*a* and *b*) at the levels indicated.

Figs. 22, 23 (× cir. 300).—Giant anchor-cells with boring muscle processes.

Fig. 24 (× cir. 300).—Fibres of boring muscle.

Fig. 25.—Diagram illustrating the connexion of the boring muscle-fibres with the anchor-cells.

Reference Letters in Figures 26–39.

ANCC, giant ' anchor '-cell ; BC, ' brain ' commissure ; BM, boring muscle ; CALC, calcareous body ; CUT, cuticle ; EGSH. egg-shell ; F, filament or tag on egg-shell ; GBL, giant blastomere ; GC, gland-cell ; HK, hooklet ; ICM, inner circular muscle-layer ; ILM, inner longitudinal muscle layer ; INB, internal nerve branch ; IVM, investing membrane of larva ; LLT, lateral longitudinal nerve-trunk ; NFI, nerve-fibre ; OBLM, oblique muscle-layer ; OCM, outer circular muscle-layer ; OLM, outer longitudinal muscle-layer ; PAR, parenchyma ; RTM, retractor muscle-fibres ; SUBC, subcuticula ; UO, opening of uterus ; YO, yolk material.

Fig. 26 (× cir. 330).—Transverse section through body-wall of A. paragonopora.

Fig. 27 (× cir. 330).—Longitudinal section through body-wall.

Fig. 28 (× cir. 980).—Early stage of growth of calcareous body.

Fig. 29 (× cir. 63).—Semi-diagrammatic figure of the anterior end of the central nervous system.

Fig. 30 (× cir. 580).—Eggs in commencement of uterus with shells and yolk.

Fig. 31 (× cir. 580).—Morula stage of embryo surrounded by investing membrane.

Fig. 32 (× cir. 580).—Early larva in longitudinal section showing one large blastomere (shell not shown).

Fig. 33 (× cir. 580).—Section through posterior end of larva showing formation of hooklet-cells.

Fig. 34 (× cir. 580).—Early larva in section showing gland-cells and hooklet-cells.

Fig. 35 (× cir. 580).—Late larva seen in optical section (the gland-cells, if present, were invisible).

Fig. 36 (× cir. 980).—Hooklet from posterior end of larva.

Fig. 37 (× cir. 580).—Three of the degenerate larvae in shells, which

occupied most of the uterus of the 280 mm. specimen of A. para-gonopoia (macerated in Marcacci's fluid).

Fig. 38 (× cir. 580).—An oval flat free larva from the same uterus (i. e. of the 280 mm. Amphilina) seen in section.

Fig. 39 (× cir. 480).—Similar degenerate larvae in shells and free larvae from the same large Amphilina, macerated in water only.

PLATE 5.

Figs. 40, 41, 42 (× 500).—Sections of early stages of development of amorphous masses, from mesentery of Macrones sp.

Figs. 43, 44 (× 112).—Sections of later young stages of development of amorphous masses.

Fig. 45 (× 35).—Section of amorphous mass elongated and slightly coiled in capsule.

Fig. 46 (natural size).—An elongated large fully-grown form of amorphous body lying free in body-cavity of fish, which would soon become transformed into an active Amphilina.

Fig. 47 (× 112).—Young cyst developed from the mesentery and enclosing degenerate larvae and disintegration products.